

# Description of the lower jaws of *Baculites* from the Upper Cretaceous U.S. Western Interior

NEAL L. LARSON<sup>1</sup> and NEIL H. LANDMAN<sup>2</sup>

<sup>1</sup>Larson Paleontology Unlimited, 12799 Wolframite Rd., Keystone, South Dakota 57751, USA.

E-mail: ammoniteguy@gmail.com

<sup>2</sup>Division of Paleontology (Invertebrates), American Museum of Natural History, 79<sup>th</sup> St. and Central Park West, New York 10024, USA. E-mail: landman@amnh.org

## ABSTRACT:

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We report the discovery of lower jaws of *Baculites* (Ammonoidea) from the Upper Cretaceous U.S. Western Interior. In the lower Campanian Smoky Hill Chalk Member of the Niobrara Chalk of Kansas, most of the jaws occur as isolated elements. Based on their age, they probably belong to *Baculites* sp. (smooth). They conform to the description of rugaptychus, and are ornamented with coarse rugae on their ventral side. One specimen is preserved inside a small fecal pellet that was probably produced by a fish. Another specimen occurs inside in a crushed body chamber near the aperture and is probably *in situ*. Three small structures are present immediately behind the jaw and may represent the remains of the gills. In the lower Maastrichtian Pierre Shale of Wyoming, two specimens of *Baculites grandis* contain lower jaws inside their body chambers, and are probably *in situ*. In both specimens, the jaws are oriented at an acute angle to the long axis of the shell, with their anterior ends pointing toward the dorsum. One of the jaws is folded into a U-shape, which probably approximates the shape of the jaw during life. Based on the measurements of the jaws and the shape of the shell, the jaws could not have touched the sides of the shell even if they were splayed out, implying that they could not have effectively served as opercula. Instead, in combination with the upper jaws and radula, they constituted the buccal apparatus that collected and conveyed food to the esophagus.

**Key words:** *Baculites*; Jaws; Upper Cretaceous; Pierre Shale; Niobrara Chalk.

## INTRODUCTION

*Baculites* are widespread in the Upper Cretaceous of North America (Klinger and Kennedy 2001). However, despite their abundance, the jaws of these ammonites are rare. Larson *et al.* (2004) and Landman *et al.* (2007) documented the lower jaws of *Baculites* from the lower Campanian Pierre Shale of South Dakota and Wyoming, the Cody Shale of Wyoming, and the Mooreville Chalk of Alabama. In their summary statement, Landman *et al.* (2007, p. 294) pointed out

that because “jaws... were undoubtedly present in all members of the Baculitidae...it is only a matter of time before they are discovered in the rest of the Upper Cretaceous.” This prediction has turned out to be true. We report here the discovery of lower jaws inside the body chambers of *Baculites grandis* Hall and Meek, 1854, from the lower Maastrichtian Pierre Shale of northeast Wyoming. We also describe new jaw material from *Baculites* sp. (smooth) from the lower Campanian Smoky Hill Chalk Member of the Niobrara Chalk of Kansas.

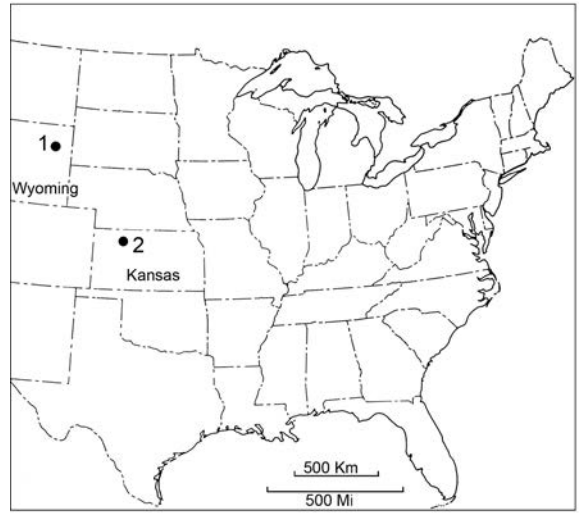
GEOLOGIC BACKGROUND

The two specimens of *Baculites grandis* with lower jaws were collected in the lower Maastrichtian *B. grandis* Zone of the Pierre Shale in Weston County, Wyoming (Text-figs 1, 2). The Pierre Shale consists of shales and silty shales deposited in the Western Interior Seaway during the early Campanian to early Maastrichtian (Landman *et al.* 2010). The informal reference section for the Pierre Shale is on the Old Woman Creek Anticline near Red Bird, Niobrara County, Wyoming (Gill and Cobban 1966). The *B. grandis* Zone has been recognized in eastern Colorado, western Kansas, eastern Montana, western South Dakota, and central and eastern Wyoming. The two specimens of *B. grandis* in this study are preserved in three dimensions with parts of their original aragonitic outer shell wall still attached.

The Niobrara Chalk consists of well-laminated to non-laminated flaky-weathering chalk (Hattin 1982). It was deposited on the eastern shelf of the Western Interior Seaway and grades progressively into less calcareous sediments toward the west. It is late Coniacian to early Campanian in age. Due to diagenesis, the calcitic aptychi of ammonites are preserved whereas the aragonitic shells of the ammonites have dissolved away, leaving only flattened internal molds (Pollastro and Scholle 1986; Everhart and Maltese 2010). The jaw material we describe is from the upper part of the Niobrara Chalk in the Smoky Hill Chalk Member in Logan County, Kansas (Text-fig. 1). The specimens occur in the lower Campanian Zone of *Hesperornis* (see Stewart 1990; Everhart 2005, p. 36, table 2.1), and based on biostratigraphic analysis (Landman *et al.* 2007, p. 262), they probably belong to *Baculites* sp. (smooth), the same species that is present in the lower Campanian Gammon Ferruginous Member of the Pierre Shale of South Dakota and the Mooreville Chalk of Alabama (Text-fig. 2).

TERMINOLOGY

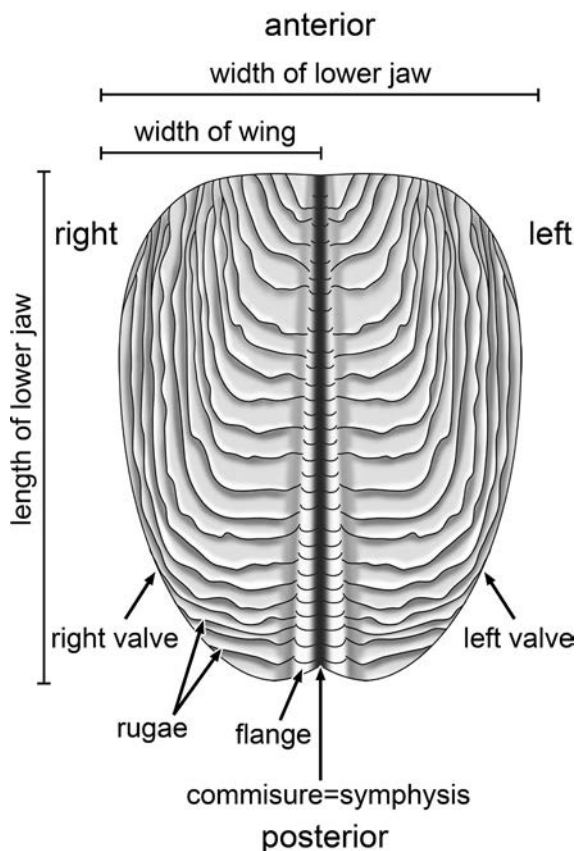
The jaws of *Baculites* conform to the morphological description of the Aptychophora (Engeser and Keupp 2002; Tanabe *et al.* 2015). The upper jaw is composed of black material that was probably originally chitin (Gupta *et al.* 2008). The lower jaw consists of two layers: an inner layer composed of black material and an outer layer composed of a pair of calcitic plates that together constitute the aptychi (or aptychus, depending on usage). The terms anterior, posterior, ventral, dorsal, left, and right refer to the jaws as they were oriented in life (Text-fig. 3). The most recently formed portion of the jaw is the posterior part. The symmetric halves of the



Text-fig. 1. Map showing localities of *Baculites* jaws from the Pierre Shale of Weston County, Wyoming, and the Niobrara Chalk of Logan County, Kansas

Maastrichtian (part)	lower	<i>Baculites clinolobatus</i>	} 1
		<i>Baculites grandis</i>	
		<i>Baculites baculus</i>	
Campanian (part)	upper	<i>Baculites eliasi</i>	} 2
		<i>Baculites jenseni</i>	
		<i>Baculites reesidei</i>	} 2
		<i>Baculites cuneatus</i>	
		<i>Baculites compressus</i>	
	<i>Didymoceras cheyennense</i>		
	<i>Exiteloceras jenneyi</i>		
	<i>Didymoceras stvensoni</i>		
	middle	<i>Baculites scotti</i>	
		<i>Baculites reduncus</i>	
<i>Baculites gregoryensis</i>			
<i>Baculites perplexus</i>			
<i>Baculites</i> sp. (smooth)			
<i>Baculites asperiformis</i>			
<i>Baculites maclearni</i>			
<i>Baculites obtusus</i>			
lower (part)	<i>Baculites</i> sp. (weak flank ribs)	} 1,2	
	<i>Baculites</i> sp. (smooth)		
	<i>Scaphites hippocrepis</i> III		

Text-fig. 2. Ammonite zonation of part of the Upper Cretaceous U.S. Western Interior (after Cobban *et al.* 2006). The brackets on the side indicate intervals containing *Baculites* jaws. 1 = this study; 2 = Landman *et al.* (2007)



Text-fig. 3. Ventral view of the lower jaws of *Baculites*. The rugaptychi are covered with coarse rugae that parallel the lateral and posterior margins (modified from Landman *et al.* 2007)

lower jaw are called the wings or valves, with the hinge or symphysis along the midline. We measured the width and length of each wing of the lower jaw, irrespective of the curvature, following the approach of Kanie (1982) and Tanabe and Fukuda (1987). Because the ends of the lower jaws are commonly broken, length is a less reliable measurement than width. We calculated jaw width as twice the wing width, so that the ratio of jaw width to jaw length is equal to twice the wing width divided by the wing length. This permits a comparison between the shape of the jaw and the shape of the ammonite whorl. The coarsely ornamented aptychus of *Baculites* has been referred to as *Rugaptychus* by Trauth (1927). We use this term, but without italics, to refer to this particular kind of morphology.

The study specimens are repositated at the American Museum of Natural History, New York (AMNH), the Rocky Mountain Dinosaur Resource Center, Woodland Park, Colorado (RMDRC), and the Natural History Museum, London (NHM).

## DESCRIPTION

### *Baculites grandis*

Only two specimens of *Baculites grandis* with jaws inside are known to exist although thousands of these specimens have been collected in the last 150 years. AMNH 102516 is a piece of a large robust body chamber 270 mm long (Text-fig. 4.1–4.4). The apertural margin is not preserved. The large size of the specimen suggests that it is probably a mature macroconch. The whorl section is subovate with a broadly rounded to somewhat flattened dorsum and a more narrowly rounded venter. The whorl width and height at the adoral end of the shell are 84.3 and 102.1 mm, respectively, so that the ratio of whorl width to height equals 0.82 (Table 1). The lower jaw is lodged in the dorsal one-half of the shell at the adoral end (Text-fig. 5). The long axis of the jaw is oriented at an angle of 45° to the long axis of the body chamber, with the anterior end of the jaw pointing toward the dorsum.

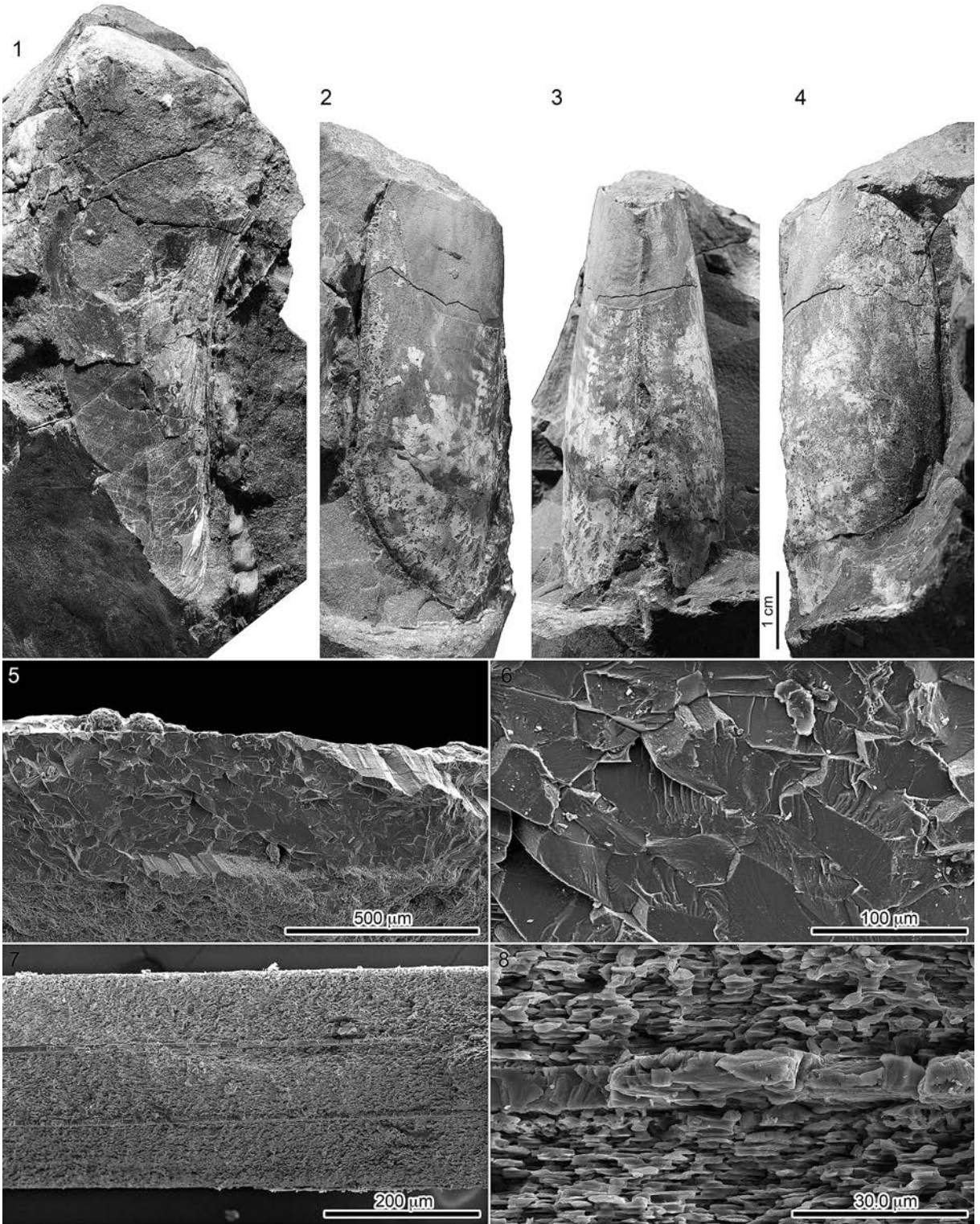
The jaw consists of the impression of a single wing with the symphysis along the right margin. Based on the fact that the surface is concave, we interpret it as the left wing. It is subquadrate in shape, with a width of 32.1 mm and a length of 77.2 mm, so that the ratio of jaw width to jaw length is 0.83. The wing is composed of a black layer 600 µm thick. In close-up, this layer exhibits a massive microstructure (Text-fig. 5.5, 5.6). The layer is ornamented with fine ridges that parallel the lateral and posterior margins. The ridges are spaced at irregular intervals with as much as 2.4 mm between successive ridges. The black layer is covered in places with patches of tan to white material. This layer is fully exposed in cross section along the symphysis and is 3.7 mm thick. It is calcitic in mineralogy with a quasi-nacreous microstructure (Text-fig. 5.7, 5.8), and probably represents the aptychus.

AMNH 102517 is a large specimen 360 mm long with part of the phragmocone and most of the body chamber intact, although the apertural margin is not preserved (Text-fig. 4.5–4.8). The specimen shows a distinctive curvature and is more slender than AMNH 102516, suggesting that it is a mature microconch. The whorl section is subovate with a broadly rounded to somewhat flattened dorsum and a more narrowly rounded venter. The whorl width and height at the adoral end of the shell are 65.5 and 91.3 mm, respectively, so that the ratio of whorl width to height equals 0.72 (Table 1). The lower jaw is lodged in the ventral one half of the shell at the adoral end (Text-fig. 5.2, 5.3, 5.4). The long axis of the jaw is oriented at an angle of 30° to the long axis of the body chamber, with the anterior









Text-fig. 5. Close-ups of the lower jaws in the body chambers of *Baculites grandis* from the lower Maastrichtian *B. grandis* Zone, Pierre Shale, Weston County, Wyoming. 1 – AMNH 102516, impression of the left wing, anterior toward the top; 2–4 – AMNH 102517, both wings of the lower jaw preserved as internal molds, anterior toward the top. 2 – Right wing. 3 – Symphysis. 4 – Left wing. 5–8 – Close-ups of the black layer and aptychus of AMNH 102516. 5, 6 – The black layer is massive in microstructure and is presumably diagenetically altered chitin. 7, 8 – The aptychus is calcitic with a quasi-nacreous microstructure

Text-fig. 4. Body chambers of *Baculites grandis* from the lower Maastrichtian *B. grandis* Zone, Pierre Shale, Weston County, Wyoming. 1–4 – AMNH 102516; 1 – Right lateral, 2 – Dorsal, 3 – Ventral, 4 – Left lateral, 5–8 – AMNH 102517, 5 – Right lateral, 6 – Doral, 7 – Ventral, 8 – Left lateral

Species	Specimen	Wing Width (mm)	Wing Length (mm)	Jaw width/length
<i>B. grandis</i>	AMNH 102516	32.1	77.2	0.83
<i>B. grandis</i>	AMNH 102517	23.6	60.9	0.78
<i>B. sp. (smooth)</i>	AMNH 66258	14.0 <sup>1</sup>	19.5	0.72
<i>B. sp. (smooth)</i>	AMNH 102500	19.4	–	–
<i>B. sp. (smooth)</i>	AMNH 102501	26.4	50.1	1.05
<i>B. sp. (smooth)</i>	AMNH 102514	22.1	–	–
<i>B. sp. (smooth)</i>	AMNH 102515	25.4	50.5	1.00
<i>B. sp. (smooth)</i>	AMNH 102528	21.5	–	–
<i>B. sp. (smooth)</i>	AMNH 102642	9.0 <sup>2</sup>	–	–
<i>B. sp. (smooth)</i>	RMDRC 07-025	16.5	35.2	0.94
<i>B. sp. (smooth)</i>	NHM C.23200	22.1	46.8	0.94

<sup>1</sup>estimate; <sup>2</sup>incomplete

Table 1. Measurements of the jaws in *Baculites grandis* from Weston County, Wyoming, and *B. sp. (smooth)* from Logan County, Kansas

end of the jaw pointing to the dorsum and the posterior end resting on the venter.

Both wings of the lower jaw are preserved as internal molds, but the anterior end is broken off. Each wing is subquadrate in shape, with a width of approximately 23.6 mm and a length of approximately 60.9 mm, so that the ratio of jaw width to jaw length is 0.78 (Table 1). The wings are folded together in a U-shape. Starting at approximately one-third of the distance from the broken anterior end, the wings are separated along the symphysis. The distance between the wings widens toward the posterior end, culminating in a gap of 9 mm. The surfaces of the wings are ornamented with weak ridges that parallel the posterior margin. They are equally spaced at distances of approximately 1 mm on the middle one-third of the right wing. The surfaces are covered in places by thin patches of white material, which are probably the remnants of the aptychus.

### *Baculites sp. (smooth)*

With the exception of two specimens (see below), the lower jaws from Kansas occur as isolated calcitic valves conforming to the description of rugaptychi (Text-fig. 6). In addition, a single partial valve occurs inside a small irregularly shaped pellet 19.8 mm in maximum length (Text-fig. 6). The valves range from 19.4 to 26.4 mm in width, with the exception of the specimen in the fecal pellet, which is incomplete and only 9.0 mm in width (Table 1). In the two most complete specimens (AMNH 102501 and 102515), the length is nearly identical, 50.1 and 50.5 mm, respectively. The ratio of jaw width to jaw length in these two specimens is also nearly the same, 1.05 and 1.00, respectively.

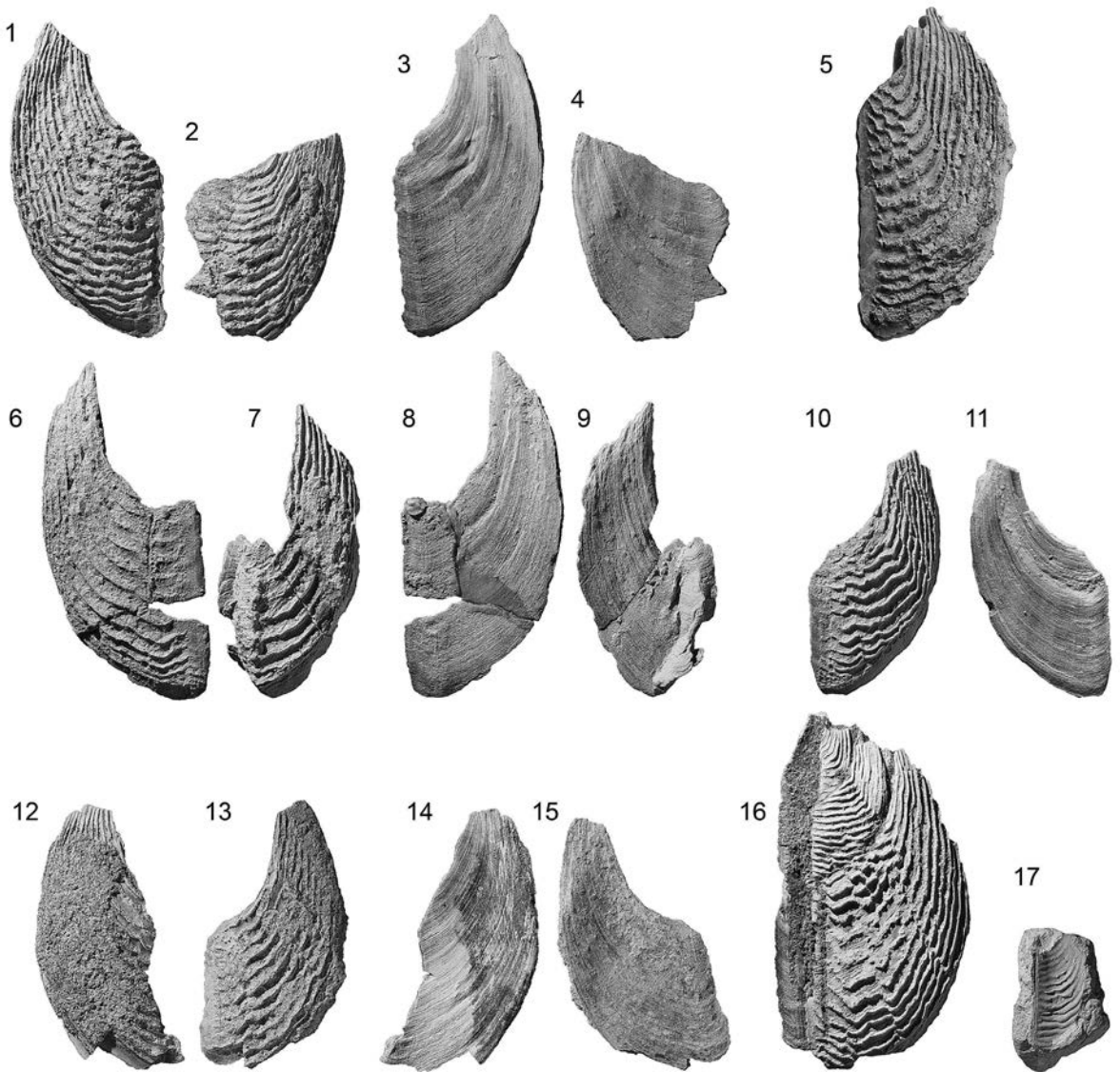
Each aptychus valve is semicircular. They are weakly convex on the ventral side and weakly concave on the dorsal side. The symphysal edge is straight and

bordered by a flange. The dorsal surface of the valve is smooth and is covered with fine lirae that parallel the lateral and posterior margins. The ventral surface is ornamented with coarse rugae that also parallel the lateral and posterior margins. In AMNH 102501, the rugae are approximately 550 µm wide at the posterior margin. They approach the symphysis at an angle of nearly 90°, forming a geniculation (Text-fig. 6). In profile, the rugae are asymmetrical with the tops of the rugae commonly bending backward (toward the anterior end) at an acute angle. The rugae do not continue onto the symphysal fold, which is covered instead by fine ridges that are convex toward the posterior.

Two specimens contain the lower jaws inside the body chamber just behind the aperture (Text-fig. 7). In RMDRC 07-025, the body chamber is crushed and incomplete with a maximum length of 76.5 mm; the whorl height at the jaw is 38.5 mm. The two valves of the rugaptychus are splayed out in butterfly fashion, and exhibit well-developed rugae (text-fig. 8-4). The width of the valves averages 16.5 mm and the length of the valves averages 35.2 mm, so that the ratio of jaw width to jaw length is 0.94. The anterior margin of both valves ends in a notch that parallels the rugae.

In AMNH 66258, the lower jaws also occur inside the body chamber just behind the aperture (Text-fig. 7). The body chamber is crushed and consists of a part and counterpart. It is 340 mm long with a whorl height at the jaw of 24.9 mm. The jaw consists of the rugaptychus, with both valves splayed out in butterfly fashion, although they slightly overlap (Text-fig. 8.1, 8.2). The surface is ornamented with weak lirae that are much finer than the rugae in the specimens described above (100 µm wide in AMNH 66258 versus 550 µm wide in AMNH 102501), suggesting that it is the dorsal surface. The anterior margin ends in a notch that parallels the lirae. The jaw is 14.0 mm wide and 19.5 mm long,





Text-fig. 6. *Rugaptychi* from the lower Campanian Smoky Hill Chalk Member, Niobrara Chalk, Logan County, Kansas. 1-4 – AMNH 102528, right and left valves; 1, 2 – Ventral; 3, 4 – Dorsal. 5 – NHM C.23200, left valve, ventral. 6-9 – AMNH 102514, right and left valves; 6, 7 – Ventral; 8, 9 – Dorsal. 10, 11 – AMNH 102501b, right valve; 10 – Ventral, 11 – Dorsal. 12-15 – AMNH 102500, right and left valves; 12, 13 – Ventral; 14, 15 – Dorsal. 16 – AMNH 102501, both valves pressed together. 17 – AMNH 102542, partial valve in a fecal pellet

so that the ratio of jaw width to jaw length equals 0.72 (Table 1). However, because the two valves slightly overlap, the jaw width is probably an underestimate and the ratio is actually higher.

Three small structures occur immediately behind the jaw in AMNH 66258 (labelled 1, 2, and 3 in Text-fig. 8). They range in maximum length from 2.5 to 5 mm and are preserved in three dimensions. They are not associated with any shell debris. Examination of their elemental composition using EDAX indicates the presence of calcium, oxygen, and phosphorous, suggesting that they are composed of apatite. In close-up, they consist of a series

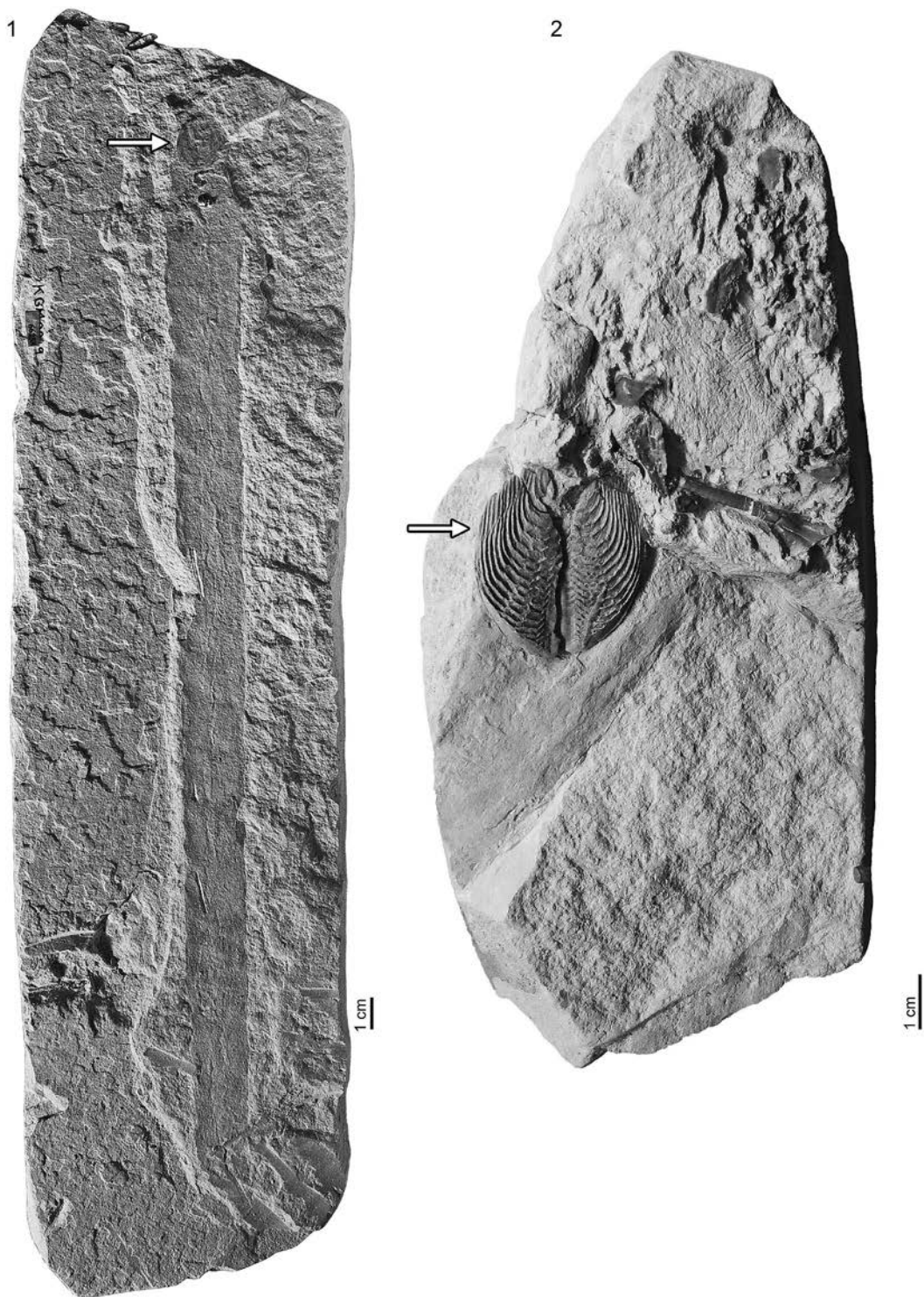
of lamellae, each of which is approximately 220  $\mu\text{m}$  thick. One of the structures (3) is surrounded by an irregular patch with a maximum extent of 13 mm.

## DISCUSSION

The lower jaws from the Smoky Hill Chalk Member of the Niobrara Chalk closely match those from the lower Campanian Mooreville Chalk of Alabama and the Gammon Ferruginous Member of the Pierre Shale. They conform perfectly to the description of

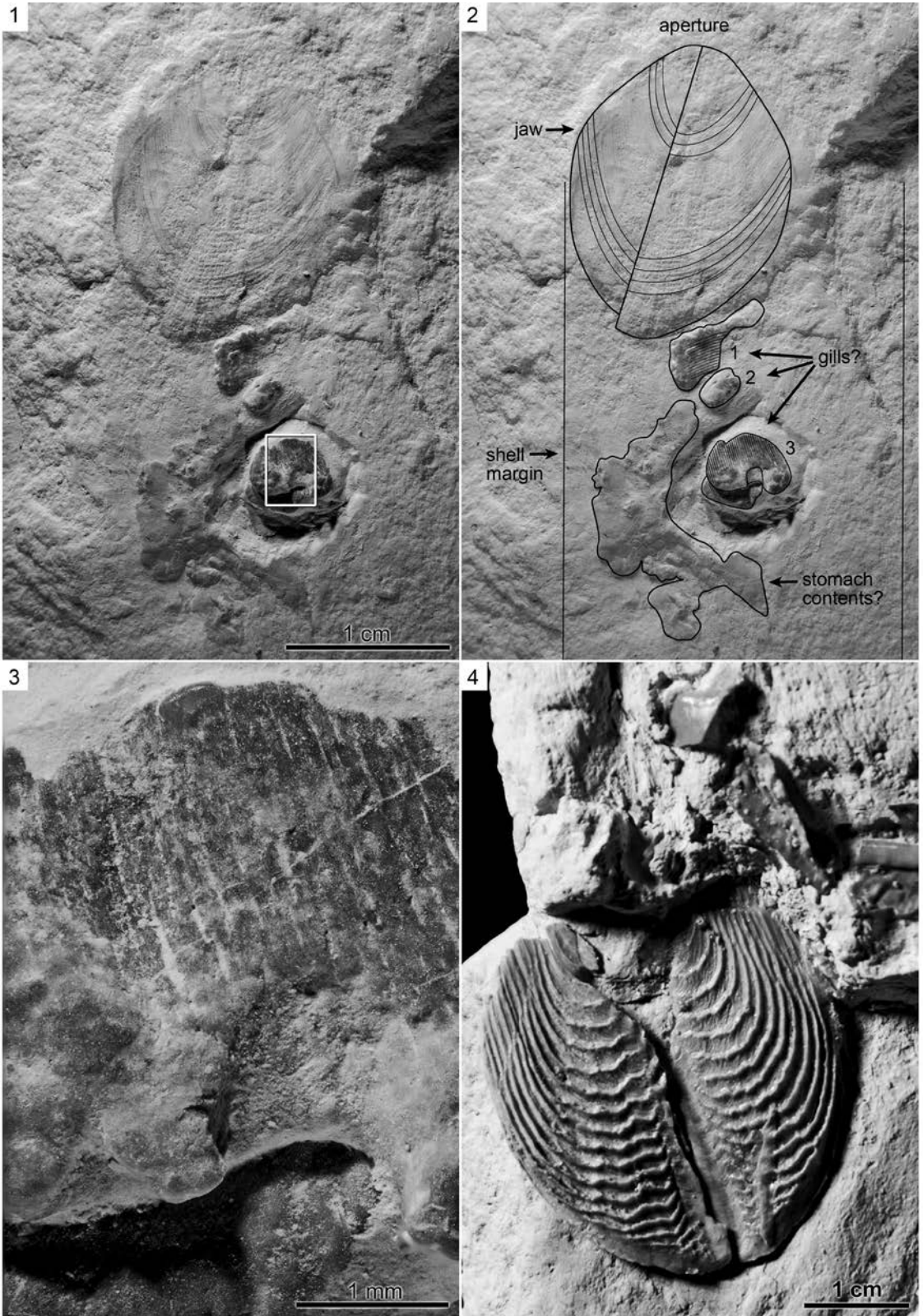
rugaptychus. They are elongate with a flange at the symphyseal edge and are ornamented with coarse rugae on their ventral side that parallel the lateral and posterior margin, approaching the symphysis almost per-

pendicularly. The only significant difference between the specimens from the Smoky Hill Chalk Member and those from the Mooreville Chalk and Pierre Shale is size (Table 1). The widths of the rugaptychi from the



Text-fig. 7. *Baculites* sp. (smooth) from the lower Campanian Smoky Hill Chalk Member, Niobrara Chalk, Logan County, Kansas. 1 – AMNH 66258, nearly complete crushed body chamber with *in situ* lower jaws (arrow). 2 – RMDRC 07-025, incomplete crushed body chamber with *in situ* lower jaws (arrow)





Text-fig. 8. *Baculites* sp. (smooth) from the lower Campanian Smoky Hill Chalk Member, Niobrara Chalk, Logan County, Kansas. **1-3** – AMNH 66258, apertural area showing the lower jaws and possible internal organs; **3** – Close-up of possible gills (?) with lamellate structure. **4** – RMDRC 07-025, close up of the lower jaws splayed out in butterfly fashion

Smoky Hill Chalk Member range from 19.4 to 26.4 mm, whereas the widths of the specimens from the Mooreville Chalk and Pierre Shale range from 6.4 to 15.8 mm (Landman *et al.* 2007, table 13.1). In addition, the maximum length of the most complete specimen of rugaptychi from the Smoky Hill Chalk Member is 50.5 mm, whereas the maximum lengths of the most complete specimens from the Mooreville Chalk and Pierre Shale are 38.6 and 37.2 mm, respectively (Landman *et al.* 2007, table 13.1). These differences suggest that the specimens of *Baculites* sp. (smooth) from the Smoky Hill Chalk Member are larger than those from the other two age-equivalent sites.

All of the rugaptychi from the Smoky Hill Chalk Member are incomplete. Even in AMNH 66258 and RMDRC 07-025 in which the jaws are preserved inside the body chamber, the anterior end is missing, forming a notch. Landman *et al.* (2007) noted this same feature in the rugaptychi from the Mooreville Chalk of Alabama, and suggested that it may be due to breakage. Alternatively, it is possible that a small gap is present at the apex between the two wings of the lower jaw, which is also mirrored in the aptychi. Such a gap has previously been described in the jaws of *Placenticerus* by Landman *et al.* (2006).

One of the rugaptychi from the Smoky Hill Chalk Member of the Niobrara Chalk is preserved inside a fecal pellet or coprolite. The pellet is irregular in shape and 19.8 mm in maximum length. Such fossils are common in this formation and were produced by sharks, fish, and marine reptiles (Hattin 1996). The small size of this coprolite suggests that it was produced by a fish. After the fish ate the ammonite, its jaws would have passed through the digestive track of the fish and been deposited as fecal matter. A similar hypothesis has been proposed to explain the abundance of ammonite jaws in a concretion from the upper Campanian Pierre Shale of South Dakota. Many of the jaws in this concretion are fragmentary and several of them are even perforated by holes (Landman and Klofak 2012, fig. 6J).

The aragonitic shells of the ammonites in the Smoky Hill Chalk Member are not preserved, precluding their use in isotopic analysis to determine the temperature of the water in which they were secreted. However, it is possible to use the calcitic rugaptychi as an alternative. Kruta *et al.* (2014) analyzed the isotopic composition of the aptychi of *Baculites* sp. (smooth) from the lower Campanian Pierre Shale and compared it to that of the shell in the same specimens. The jaws and shells are not composed of the same mineralogy (calcite versus aragonite) and are not secreted by the same tissue, thus representing independent systems. Nevertheless, the calculated temperatures of well-preserved jaws matched

those of well-preserved shells in the same specimens. Thus, provided that the aptychi in the Smoky Hill Chalk Member are well preserved, they can be used as temperature proxies in lieu of the actual ammonite shells.

The presence of *in situ* jaws, that is, jaws preserved inside the body chamber, in the two specimens of *Baculites grandis* allows an assessment of the correspondence between the shape of the jaws and the shape of the whorl section (Table 1). In both specimens, the correspondence is perfect. In AMNH 102516, the ratio of jaw width to length is 0.83 and the ratio of whorl width to height is 0.82. In AMNH 102517, the ratio of jaw width to length is 0.78 and the ratio of whorl width to height is 0.72. Thus, not surprisingly, in both specimens, the shape of the jaws matches the shape of the whorl section. This has also been demonstrated in other ammonites, e.g., scaphites (Landman and Waage 1993).

In contrast, the width and length of the jaws do not match the width and height of the whorl section. In AMNH 102516, the whorl width and height are 84.3 and 102.1 mm, respectively, whereas the jaw width and length are 64.2 and 77.2 mm, respectively. In AMNH 102717, the whorl width and height are 65.5 and 91.3 mm, respectively, whereas the jaw width and length are 47.2 and 60.9 mm, respectively. Based on these comparisons, even if the jaws were fully splayed out in each specimen, they would not have touched the sides of the shell. Thus, these data are inconsistent with the hypothesis that aptychi served as ammonite opercula closing off the aperture (for recent discussions about the possible functions of aptychi, see Parent and Westermann [2014] and Tanabe *et al.* [2015]).

It is difficult to reconstruct the original position of the jaws during life due to a variety of taphonomic factors. However, the two specimens of *Baculites grandis* provide some clues. In each specimen, the long axis of the lower jaw is oriented at an acute angle to the long axis of the body chamber (45° in AMNH 102516 and 30° in AMNH 102517), with the anterior end of the jaw pointing toward the dorsum. This is similar to the position of the jaws inside the body chambers of *Baculites* sp. (smooth) from the Pierre Shale of South Dakota studied by Landman *et al.* (2007). The lower jaws in AMNH 102517 are folded into a U-shape, which probably approximates the position of the lower jaws during life.

In the specimens of *Baculites grandis* with lower jaws inside the body chamber, the upper jaws are not visible. It is possible that they could be detected with CT-scanning, especially in AMNH 102517 in which the lower jaws are folded into a U-shape. Kruta *et al.* (2011) used this technique to investigate the buccal apparatus in *Baculites* sp. (smooth) from the Pierre Shale of South Dakota. Their reconstructions revealed



1) a lower jaw covered with two calcareous plates, 2) a smaller upper jaw (less than one-half the length of the lower jaw), and 3) a radula nestled between the upper and lower jaws consisting of nine small delicate teeth with a tall, sabrelike marginal tooth. Klug *et al.* (2012) documented the same features in their study of baculitid ammonites from the Upper Cretaceous of Germany (for recent discussions about the morphology of the buccal apparatus in ammonites, see Kruta *et al.* [2015] and Tanabe *et al.* [2015]).

The structures preserved just behind the jaw in the specimen of *Baculites* sp. smooth are intriguing and require further study. They are unlikely to represent foreign debris that was transported into the body chamber because they are not associated with any other material. We interpret them instead as the remains of internal organs. Based on an examination of their elemental composition, they are probably made up of apatite. They consist of a series of lamellae, each of which is approximately 220  $\mu\text{m}$  wide. This morphology most closely matches that of the gills in modern cephalopods (Young and Vecchione 2002, 2004). Gills have been preserved as fossils in a number of cephalopods, suggesting that these organs are possibly resistant to decay (e.g., Lehmann 1985). The most convincing example is that of Reitner (2011) who described the fossilized gill apparatus of a Jurassic belemnoid from Germany. We therefore tentatively identify these structures as the remains of the gills, but note that in modern cephalopods nidamental glands and oviducal glands are also composed of lamellae (M. Vecchione, pers. comm., 2016). In analogy with the diagrams published by Klug and Lehmann (2015, fig. 12.3), we tentatively interpret the irregularly shaped splotch around the gills (?) as the digestive gland or stomach.

## SUMMARY

The lower jaws of *Baculites* are subquadrate in shape. Like the lower jaws of the rest of the Aptychophora, they consist of two wings that meet along the symphysis. The inner layer is black and was probably originally composed of chitin. The outer layer is calcitic and is called the rugaptychus. In combination with the upper jaws and radula, they form the buccal mass and occupy the adoral part of the body chamber.

*Baculites* are common in the U.S. Western Interior but their jaws are rare due to post-mortem destruction. With the discoveries reported here, the lower jaws of *Baculites* are now known from the lower and upper Campanian and the lower Maastrichtian of North America. Further field collecting may yet yield more jaw specimens and fill in the missing gaps.

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## REFERENCES

- Cobban, W.A., Walaszczyk, I., Obradovich, J.D. and McKinney, K.C. 2006. A USGS zonal table for the Upper Cretaceous Middle Cenomanian–Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages. *U.S. Geological Survey Open-File Report*, **2006-1250**, 1–46.
- Engeser, T. and Keupp, H. 2002. Phylogeny of aptychi-possessing Neoammonoidea (Aptychophora nov., Cephalopoda). *Lethaia*, **24**, 79–96.
- Everhart, M.J. 2005. Oceans of Kansas: A natural history of the Western Interior Seaway., pp. 1–344. Indiana University Press; Bloomington, Indiana.
- Everhart, M.J., and Maltese, A. 2010. First report of a heteromorph ammonite, cf. *Glyptoxoceras*, from the Smoky Hill Chalk (Santonian) of western Kansas, and a brief review of Niobrara Chalk cephalopods. *Transactions of the Kansas Academy of Science*, **113**, 64–70.
- Gupta, N.S., Briggs, D.E.G., Landman, N.H., Tanabe, K., and Summons, R.E. 2008. Molecular structure of organic components in cephalopods: evidence from oxidative cross linking in fossil marine invertebrates. *Organic Geochemistry*, **39**, 1405–1414.
- Hall, J. and Meek, F.V. 1854. Description of new species of fossils, from the Cretaceous formations of Nebraska, with observations upon *Baculites ovatus* and *B. compressus*, and the progressive development of the septa in *Baculites*, *Ammonites* and *Scaphites*. *Memoirs of the American Academy of Arts and Sciences New Series*, **5(2)**, 379–411.

- Hattin, D.E. 1982. Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. *Kansas Geological Survey Bulletin*, **225**, 1–108.
- Hattin, D.E. 1996. Fossilized regurgitate from Smoky Hill Member of Niobrara Chalk (Upper Cretaceous) of Kansas, USA. *Cretaceous Research*, **17**, 443–450.
- Kanie, Y. 1982. Cretaceous tetragonitid ammonite jaws: a comparison with modern *Nautilus* jaws. *Transactions and Proceedings of the Palaeontological Society of Japan. New Series*, **125**, 239–258.
- Klinger, H.C. and Kennedy, W.J. 2001. Stratigraphic and geographic distribution, phylogenetic trends and general comments on the ammonite family Baculitidae Gill, 1871 (with an annotated list of species referred to the family). *Annals of the South African Museum*, **107**, 1–290.
- Klug, C., Riegraf, W. and Lehmann, J. 2012. Soft-part preservation in heteromorph ammonites from the Cenomanian-Turonian event (OAE 2) in the Teutoburger Wald (Germany). *Palaeontology*, **55**, 1307–1331.
- Klug, C. and Lehmann, J. 2015. Soft part anatomy of ammonoids: Reconstructing the animal based on exceptionally preserved specimens and actualistic comparisons. In: Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R.H. (Eds), *Ammonoid paleobiology: From anatomy to ecology*. Springer, New York, pp. 507–529.
- Kruta I., Landman, N.H. and Cochran, J.K. 2014. A new approach for the determination of ammonite and nautilid habitats. *PLoS ONE* **9**(1), e87479 doi:10.1371/journal.pone.0087479
- Kruta, I., Landman, N.H., Rouget, I., Cecca, F. and Tafforeau, P. 2011. The role of ammonites in the Mesozoic marine food web revealed by jaw preservation. *Science*, **331**, 70–72.
- Kruta, I., Landman, N.H. and Tanabe, K. 2015. Ammonoid radula. In: Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R.H. (Eds), *Ammonoid paleobiology: From anatomy to ecology*. Springer, New York, pp. 485–505.
- Landman, N. H. and Klofak, S.M. 2012. Anatomy of a concretion: Life, death, and burial in the Western Interior Seaway. *Palaios*, **27**, 672–693.
- Landman, N.H., Larson, N.L. and Cobban, W.A. 2007. Jaws and radula of *Baculites* from the Upper Cretaceous (Campanian) of North America. In: Landman, N.H., Davis, R.A. and Mapes, R.H. (Eds), *Cephalopods present and past: New insights and fresh perspectives*, Springer, New York. pp. 257–298.
- Landman, N.H., Tsujita, C.J., Cobban, W.A., Larson, N.L., Tanabe, K. and Flemming, R.L. 2006. Jaws of Late Cretaceous placenticeratid ammonites: How preservation affects the interpretation of morphology. *American Museum Novitates*, **3500**, 1–44.
- Landman, N.H. and Waage, K.M. 1993. Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills Formation in South Dakota and Wyoming. *Bulletin of the American Museum of Natural History*, **215**, 1–257.
- Landman, N.H., Kennedy, W.J., Cobban, W.A. and Larson, N.L. 2010. Scaphites of the “*nodosus* group” from the Upper Cretaceous (Campanian) of the Western Interior of North America. *American Museum of Natural History Bulletin*, **342**, 1–242.
- Larson, N.L., Landman, N.H., Kennedy, W.J. and Cobban, W.A. 2004. *Baculites* jaws from the Campanian (Late Cretaceous) of North America. Sixth International Symposium, Cephalopods—Present and Past, Abstracts, 105.
- Lehmann, U. 1985. Zur Anatomie der Ammoniten: Tintenbeutel, Kiemen, Augen. *Paläontologisches Zeitschrift*, **59**, 99–108.
- Parent, H. and Westermann, G. 2014. Ammonite aptychi: Functions and role in propulsion. *Geobios*, **47**, 45–55.
- Pollastro, R.M. and Scholle, P.A. 1986. Diagenetic relationships in hydrocarbon-productive chalk, the Cretaceous Niobrara Formation. In: Mumpton, M.A. (Ed.), *Studies in diagenesis*. *U.S. Geological Survey Bulletin*, **1578**, 219–236.
- Reitner, J. 2011. Preserved gill remains in *Phragmot euthis conocauda* (Quenstedt, 1846–49) (Toarcian, Southern Western Germany). *Berliner Paläobiologische Abhandlungen*, **10**, 289–295.
- Stewart, J.D. 1990. Niobrara Formation vertebrate stratigraphy. In: Bennett, S.C. (Ed.), *Niobrara Chalk Excursion Guidebook*, The University of Kansas Museum of Natural History and the Kansas Geological Survey, pp. 19–30.
- Tanabe, K., Kruta, I., and Landman, N.H. 2015. Ammonoid buccal mass and jaw apparatus. In: Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R.H. (Eds), *Ammonoid paleobiology: From anatomy to ecology*, pp. 429–484. Springer; New York.
- Tanabe, K. and Fukuda, Y. 1987. The jaw apparatus of the Cretaceous ammonite *Reesidites*. *Lethaia*, **20**, 41–48.
- Trauth, F. 1927–1936. Aptychenstudien I–VIII. *Annalen des Naturhistorischen Museum in Wien*, **41**, 171–259 (1927); **42**, 121–193 (1928); **44**, 329–411 (1930); **45**, 17–136 (1931); **47**, 127–145 (1936).
- Young, R.E. and Vecchione, M. 2002. Evolution of the gills in the Octopodiformis. *Bulletin of Marine Science*, **71**, 1003–1018.
- Young, R.E. and Vecchione, M. 2004. Cephalopod Gills – Tree of Life Web Project: <http://to/web.org>.